

Evaluating reserves for species richness and representation in northern California

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ABSTRACT

The Klamath-Siskiyou forests of northern California and southern Oregon are recognized as an area of globally outstanding biological distinctiveness. When evaluated at a national or global level, this region is often, necessarily, considered to be uniformly diverse. Due to large variation in biotic and abiotic variables throughout this region, however, it is unlikely that biological diversity is uniformly distributed. Furthermore, land management decisions nearly always occur at spatial scales smaller than this entire region. Therefore, we used field data from a random sampling design to map the distribution of local and regional richness of terrestrial molluscs and salamanders within northern California's portion of the Klamath-Siskiyou region. We also evaluated the protection afforded by reserves established for varying reasons (e.g. for inspiration and recreation for people vs. species conservation) to hotspots of species richness and species representation of these taxa. No existing reserves were created with these taxa in mind, yet it was assumed that reserves established largely around considerations for the northern spotted owl (*Strix occidentalis caurina*) would afford adequate protection for many lesser-known species. Species of terrestrial molluscs and salamanders share two general features: (1) they have extremely low vagility, and (2) they are often associated with moist, cool microclimates. Existing reserves disproportionately included areas of hotspots of species richness for both taxa, when hotspots included the richest c. 25% of the area, whereas non-reserved lands contained greater than expected areas with lower species richness. However, when a more strict definition of hotspot was used (i.e. the richest c.10% of areas), local hotspots for both taxa were not disproportionately found in reserves. Reserves set aside largely for human aesthetics and recreation and those set aside for biodiversity both contributed to the protection of areas with high (greatest 25%) species richness. Existing biodiversity reserves represented 68% of mollusc species and 73% of salamander species, corresponding to the 99th and 93rd percentiles, respectively, of species representation achieved by simulating a random distribution of the same total area of reservation. Cumulatively, however, reserves set aside for inspiration and biodiversity represented 83% of mollusc species and 91% of salamander species. The existing reserves provide conservation value for terrestrial molluscs and salamanders. This reserve network, however, should not be considered optimal for either taxa.

Keywords

Conservation planning, hotspot, mollusc, Northwest Forest Plan, representation, reserves, salamander, species richness, umbrella species.

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INTRODUCTION

Many evaluations of the distribution of species richness have occurred at scales larger than ecological regions and often portray large regions as being biologically uniform (e.g. Davis *et al.*, 1998; Ricketts *et al.*, 1999; California Department of Fish & Game, 2003; Orme *et al.*, 2005). At the spatial scale that most land management

decisions are made, an understanding of the local distribution of species richness has practical consequences. The decision to allow or restrict various land uses (e.g. timber harvesting, recreation, road building), as well as the location and distribution of potential conservation areas, could be influenced by such knowledge.

Conservation plans designed largely around umbrella species have often been evaluated for hypothetical reserves (see review

by Roberge & Angelstam, 2004), and have been met with limited success (Andelman & Fagan, 2000; Roberge & Angelstam, 2004). However, Caro (2003) found that actual reserves designed around umbrella species (large mammals) in East Africa were effective at conserving other 'background' species. Roberge & Angelstam (2004) noted that the greatest challenge to evaluating the umbrella species concept was data from actual, not hypothetical, reserves designed around umbrella species. Herein, we provide such an evaluation for a conservation plan designed largely around the northern spotted owl (*Strix occidentalis caurina*; Merriam, 1898).

We evaluated the distribution of terrestrial mollusc and salamander species richness and the protection afforded by two reserve types and non-reserved lands to hotspots of species richness and to species representation. We also evaluated the concordance of richness patterns of terrestrial molluscs and salamanders. In the Pacific Northwest of the USA, the Northwest Forest Plan (hereafter NFP; USDA/USDI, 1994) was developed as a large-scale (c. 10 million ha) ecosystem management plan; striving to provide a predictable and sustainable timber supply and to adequately protect species. Prior to the NFP, most reserves (e.g. Wilderness Areas) were primarily set aside for their inspirational and recreational values. Collectively, we refer to such reserves as *pre-NFP reserves*. More recently, through the NFP, the US government created a network of 'late successional reserves' and 'riparian reserves' (USDA/USDI, 1994). The late successional reserve network was designed, largely, based on quantitative information and conservation considerations of the northern spotted owl as well as, generally, qualitative, expert-based considerations of > 1000 other species; including some terrestrial molluscs and salamanders. Riparian reserves are buffer areas adjacent to streams and rivers (see USDA/USDI, 1994). We refer to the late successional reserves and riparian reserves, collectively, as *NFP reserves*. NFP reserves included pristine areas as well as previously harvested areas. Land management activities within NFP reserves must generally be consistent with the goal of facilitating late-successional forest conditions more rapidly than would otherwise occur. We are unaware of any concerted attempt to evaluate the protection-afforded centres of species richness or species representation by various reserves and non-reserves within the NFP area. Efforts such as this are not novel for conservation biologists (e.g. Scott & Jennings, 1997; Wright *et al.*, 2001; Cantú *et al.*, 2004; Fox & Beckley, 2005), but our approach differs from most others in that our estimates are not based on the collation of existing data (e.g. museum collections, natural diversity databases), but on a planned field sample across a large area occupied by terrestrial molluscs and salamanders.

We had access to a new survey data set that described the distributions of 47 species of molluscs and 11 species of salamanders in north-western California (see Molina *et al.*, 2003; Dunk *et al.*, 2004). Because of the much larger number of mollusc species than salamander species, the results of combined mollusc and salamander richness would likely be driven by molluscs alone. Therefore, we evaluated each taxon separately. We had three goals. Our first goal was to identify hotspots of local and regional richness for each taxon (see Methods for definitions of local and regional richness). Local richness is ultimately limited by the regional richness surrounding a local site. However, due to the

varying histories of impacts (e.g. timber harvest, fire) across our study area, we could conceive of several factors that could 'uncouple' a strong correlation between local and regional richness, such that hotspots of local richness *could* be found outside of hotspots of regional richness. Our second goal was to evaluate the concordance of local and regional distributional patterns between these disparate taxa to determine whether either taxon would be a good surrogate for the diversity of the other (e.g. Moritz *et al.*, 2001). Although not closely related taxonomically, terrestrial molluscs and terrestrial salamanders share two key features: (1) both have low vagility and (2) both appear to need microclimates that provide abundant moisture during, at least, a part of the year, and thus one might expect them to show similar geographical patterns of diversity. Our third goal was to compare how the pre- and NFP reserves protect hotspots of species richness, and represent species composition, within these taxa, even though these were not explicitly considered when either reserve type was established. Ferrier (2002) noted that little research effort has been devoted to evaluating how well surrogates (the spotted owl in this case) perform as a basis for selecting conservation areas that are representative of biodiversity as a whole. Conservation of hotspots alone may neglect other important and valued attributes of an area's biota (Kareiva & Marvier, 2003), including protection of rare (Lennon *et al.*, 2004) or endemic (Orme *et al.*, 2005; Stohlgren *et al.*, 2005) species; as well as species representation and persistence (Margules & Pressey, 2000). Hence, we also evaluated the degree to which regional hotspots for each taxon sheltered the rarest species within each taxon. Our analyses can be considered an evaluation of the protections the spotted owl provides as an umbrella for hotspots of mollusc and salamander richness and species representation within each taxon.

METHODS

Study area

Mollusc and salamander surveys were conducted within c. 2.2 million ha of the Klamath-Siskiyou forests of northern California (Klamath Bioregion; Welsh, 1994), within the boundaries of the Klamath, Mendocino, Six Rivers, and Shasta-Trinity national forests. Climatic conditions change from wet and moderate temperatures, to dry and variable temperatures (summer highs and winter lows) from northwest to southeast. The study area was almost entirely within the North Coast Floristic Region (Barbour & Major, 1988) and included the Klamath Mountains, northern California Coast Range, southern Cascades, and sections of the Sierra forest ecological subregions (Bailey, 1995). The northern portion of the study area represents the southern extent of the 'Pacific Northwest' and may receive annual precipitation of > 350 cm (Schoenherr, 1992). Vegetation in the Klamath Mountains is dominated by Douglas-fir (*Pseudotsuga menziesii*)/mixed evergreen-hardwood forests. At higher elevations, white fir (*Abies concolor*) and red fir (*Abies magnifica*) dominate. To the east, the study area becomes more xeric and contains portions of the volcanic Cascade Mountains where vegetation changes from more conifer-dominated to conifer-hardwood, dominated by

pine (*Pinus ponderosa* and *Pinus sabiniana*) and deciduous oaks (*Quercus garryana* and *Quercus kelloggii*). There are also north–south transitions with northern portions of the study area generally receiving more rain and having lower summer high temperatures than southern areas. Southern portions of the study area are more mixed–conifer/hardwood (with low conifer abundance) or pure hardwood than northern areas, as well as having more brush-dominated areas. Elevation in the study area ranged from c. 100 m to 3000 m. We estimated that 39% of the study area was non-reserved, 38% NFP reserves, and 23% pre-NFP reserves.

Mollusc and salamander sampling

Mollusc sampling took place during 1999 and 2000 and salamander sampling during 2000. A total of 308 1-ha Forest Inventory and Analysis (FIA; Roesch & Reams, 1999; US Department of Agriculture Forest Service 2000; <http://fia.fs.fed.us/>) plots were sampled for molluscs in 1999 and 2000, and 234 (a subset of the 308) were sampled for salamanders in 2000. Plots were randomly selected from c. 1100 FIA plots that exist on an c. 5.5-km grid throughout the study area. FIA plot vegetation data are periodically gathered and used to assist in planning and monitoring forest structure and plant communities at broad scales (e.g. a region or a national forest). We stratified samples by national forest to ensure that each forest was sampled proportionate to its area.

Each FIA plot was sampled twice for molluscs and salamanders, with a minimum of 10 days between surveys. Surveys were conducted only if the daytime temperature was $> 5^{\circ}\text{C}$, and soil was moist as determined by touch. Surveys began with crews walking through the 1-ha plot and identifying structural features that were likely to provide mollusc habitat (e.g. downed wood), after which two types of focused searches were conducted. *Area* searches targeted the most likely mollusc habitat in each 1-ha plot by thoroughly inspecting a feature (e.g. downed wood, rock, fern) and the area likely to contain molluscs within a 5 m-radius (80 m^2) surrounding that feature. One 20-min time-constrained area search was conducted (all times represent person–minutes; 1 person for 20 min = 2 people for 10 min each). *Point* searches were 40-min time-constrained searches where surveyors visited many locations within the plot, spending a maximum of 3 min at any location before moving on. Thus, each plot was sampled twice, for 1 h each time. Salamander sampling took place in 2000 only, and happened concomitant to mollusc sampling (see Dunk *et al.*, 2002, 2004 for more details on mollusc sampling and Welsh *et al.* (in press) for more details on salamander sampling).

Of the 308 plots sampled for molluscs, 139 (45.3%) were in non-reserved, 102 (33.2%) were in NFP reserves, 66 (21.5%) were in pre-NFP reserves, and one was on private land, which was excluded from the analyses. Of the 234 plots sampled for salamanders, 100 (42.7%), 82 (35.0%), and 52 (22.2%) were in non-reserved, pre-NFP reserves, and NFP reserves, respectively.

Estimating species richness

Local richness was the total number of species detected at each 1-ha plot. Regional richness was estimated as the number of

individual species' geographical ranges that overlapped at each square kilometre in the study area (similar to the method used by Caley & Schluter, 1997). To estimate geographical ranges of species found at ≥ 2 locations, we used nonparametric logistic regression, a subset of generalized additive models with loess smoothing functions (Cleveland, 1985), to create occurrence probability surfaces for each species. Spatial (UTM) coordinates were the only covariates entered into these models, with presence–absence as the binary response variable. We used Akaike's Information Criterion (AIC; Akaike, 1973) to evaluate different span values (smoothing parameters; Chambers & Hastie, 1997) ranging from 0.20 to 0.80, and chose the span that resulted in the smallest AIC value. We then estimated the geographical range as the area within the 0.025 probability contour (i.e. all 1 km^2 areas with ≥ 0.025 probability of occurrence were considered to be within the species' geographical range). The 0.025 probability contour was chosen based on the findings of Dunk *et al.* (2004), who found that 100% of their sample locations for molluscs and 94% of the locations from an independent data set fell within this contour. These estimates were conducted for the 32 species of molluscs and seven species of salamanders, and the resulting estimates are relevant only to our study area. The geographical ranges of some species, particularly salamanders, were known to extend beyond the study area.

Because our approach to estimating regional richness required an estimate of geographical range for each species, it was necessary to do so for species for which there were only a few locations. To give some geographical range (area) value to mollusc species that were found only once ($n = 15$), we produced a linear regression model relating the number of locations at which a species was detected to the geographical range size for 32 species found at 2 to 55 locations ($r^2 = 0.6812$), then extrapolated backward to a single location. This resulted in an estimate of 612 km^2 that, when portrayed as a circle, had a radius of c. 14 km. Thus, any location within 14 km of a species that was discovered at only one location was treated as part of its geographical range. The number of salamander species was too small to use for this same method of extrapolating geographical ranges for very rare species. We did not want our species-rich data set to have rarer species unrepresented, and reasoned that including even rough estimates of those species' ranges would more accurately represent regional richness than would eliminating such species from our analyses.

Defining hotspots

Hotspots have been defined in various ways (Harcourt, 2000), thus we evaluated two of the more common definitions: (1) those areas/locations with greater species richness than 90% of other areas/locations (hotspots₉₀), and (2) those areas with greater species richness than 75% of other areas/locations (hotspots₇₅). The first definition is similar to that used by Prendergast *et al.* (1993) and Williams *et al.* (1996), whereas the second was used by Harcourt (2000) and is also similar to the thresholds used by Tardif & Des Granges (1998). For both hotspots₉₀ and hotspots₇₅, we attempted to get as close as possible to the '90' and '75' targets.

Evaluating overlap of hotspots of regional richness with rare species

We considered rare species to be those that were detected at ≤ 2 sample plots. Although many other species from our study can legitimately be considered rare, we chose a conservative definition of rarity. We evaluated the degree to which rare species were included in the boundaries of hotspots₉₀ and hotspots₇₅. Because the estimates of regional richness were derived from each of the individual species' locations (see above), they were not independent measures. Thus, we did not use formal statistical analyses. Instead we compared the observed number of rare species to the number expected to be in a hotspot if they were distributed randomly.

Evaluating species richness relative to reserved and unreserved lands

The regional and local richness data were used to evaluate the overlap of hotspots₉₀ and hotspots₇₅ with pre-NFP and NFP reserves and non-reserved lands (hereafter, we refer to the two reserve types and non-reserved lands collectively as land allocations). We tested the association of local richness hotspots₉₀ and hotspots₇₅ to land allocations using the Cochran–Mantel–Haenszel statistic (CMH; Agresti, 1996) with each of the four national forests as strata. The evaluation of the association of regional richness to land allocations was based on the ratios of observed and expected areas of each land allocation within each species richness category. We evaluated whether each land allocation represented the same percentage of each regional richness category as it did of the entire study area. Thus, values less than 100% represent less richness than expected by chance and values more than 100% represent more richness than expected by chance.

Evaluating species representation

We compared species representation in NFP reserves, by taxon, to species representation in the locations of 100 simulated reserves to determine the likelihood of the observed species representation in reserves occurring by chance. For the 100 simulations, we first excluded all areas of pre-NFP reserve, as they were unable to be considered for inclusion in the NFP reserve network. Second, we drew a random sample of plots occurring within NFP reserve and unreserved lands equal in size to the sample of plots that we surveyed in NFP reserves ($n = 76$ and 65 for molluscs and salamanders, respectively). The 100 simulated reserves were ranked first in order of species representation and second by the number of species that had 10, 25, 50, and 75% of their total observations fall within reserves. The latter ranking served as a 'tie-breaker'; when species representation was equal, a simulation that resulted in more species' locations being in reserves ranked higher than simulation with a smaller number in reserves. The observed species representation found in reserves was compared to the distribution resulting from the simulations. That is, if only 5 of 100 simulated reserves resulted in better species representation than the actual reserves achieved, the observed pattern would be unlikely to be

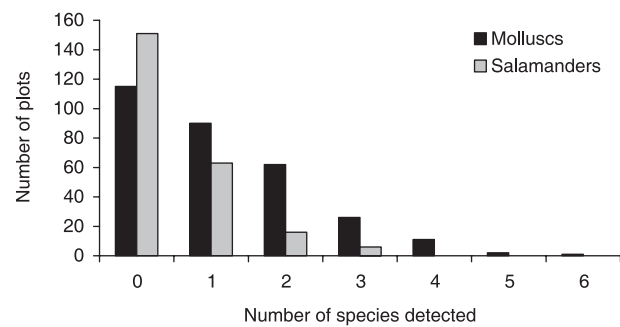


Figure 1 Frequency distribution of mollusc and salamander local species richness.

obtained by chance (5% chance). If the species representation within NFP reserves was no better than expected by chance, then the actual species representation should fall somewhere in the middle of the distribution observed from the 100 simulated reserves. The lower the likelihood that the observed species representation was due to chance, the more likely that reserves designed largely to protect the northern spotted owl serve as a good proxy for species representation of these other taxa.

RESULTS

Local richness hotspots

A total of 47 mollusc species and 11 salamander species were detected. Mean local richness for molluscs was 1.15 ($SD = 1.19$) and ranged from 0 to 6 (Fig. 1). Mean local richness for salamanders was 0.48 ($SD = 0.74$) and ranged from 0 to 3 species (Fig. 1).

The local richness hotspots₉₀ and hotspots₇₅ for molluscs were those 14 plots (4.5% of all plots), where ≥ 4 species were detected, and 103 plots (33.6% of all plots), where ≥ 2 species were detected, respectively (Fig. 2a). Ninety plots had one species, and no molluscs were detected at 115 plots. There was no difference between expected and observed frequencies of occurrence of local mollusc richness hotspots₉₀ with land allocations (CMH statistic = 1.88, 2 d.f., $P = 0.3913$). In contrast, the local mollusc richness hotspots₇₅ were disproportionately associated with land allocations (CMH statistic = 8.71, 2 d.f., $P = 0.0129$). This association was largely due to more hotspot₇₅ plots occurring in NFP reserves and pre-NFP reserves and fewer occurring in non-reserved than expected.

The local richness hotspots₉₀ and hotspots₇₅ for salamanders were those 22 plots (9.4% of all plots) where ≥ 2 species were detected and those 85 plots (36.3% of all plots) where ≥ 1 species was detected, respectively (Fig. 2b). No salamanders were detected at 149 plots. Our comparison of these salamander local richness categories revealed no association of hotspots₉₀ with land allocations (CMH statistic = 0.03, 2 d.f., $P = 0.987$). In contrast, there was a significant association of local salamander richness hotspots₇₅ with land allocations (CMH statistic = 10.32, 2 d.f., $P = 0.006$). Similar to the molluscs, this association was due to more local hotspot₇₅ plots than expected in NFP reserves and pre-NFP reserves and fewer hotspot₇₅ plots than expected in non-reserved.

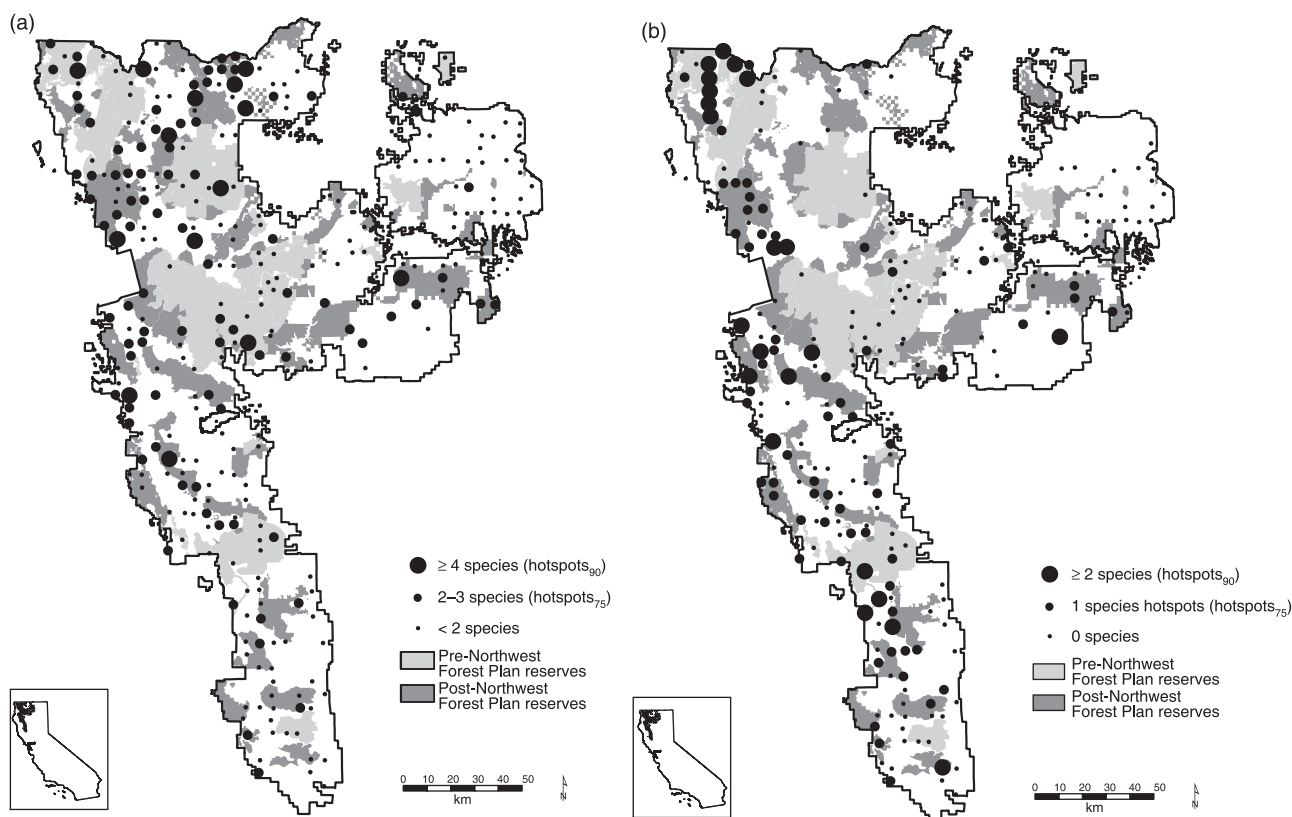


Figure 2 Distribution of (a) local mollusc and (b) local salamander richness throughout the study area. Note: riparian reserves are not portrayed on these maps. Inset shows study area within California, USA.

Regional richness

For molluscs, regional richness peaked at 19. The portion of our study area with ≥ 16 overlapping geographical ranges represented 5.1% of the study area (*c.* 1000 km²) and delineated the hotspots₉₀ of mollusc regional richness. The portion of the study area with ≥ 14 overlapping geographical ranges represented 20.4% of the study area and delineated the mollusc hotspots₇₅ (Fig. 3a). Regional richness of salamanders varied from 0 to 5 species. The portion of the study area with five species encompassed 3.7% of the study area and delineated the hotspots₉₀ of salamander regional richness. The area with ≥ 4 overlapping geographical ranges represented 19.1% of the study area and delineated the salamander hotspots₇₅ (Fig. 3b).

NFP reserves, pre-NFP reserves, and non-reserved lands represented 92, 134, and 88% of the expected regional mollusc richness hotspots₉₀, respectively. In the regional mollusc hotspots₇₅, NFP reserves, pre-NFP reserves, and non-reserved lands represented 121, 112, and 73% of their expected area, respectively. Thus, mollusc hotspots (especially hotspots₇₅) had more reserved land than expected and less non-reserved land.

Within the regional salamander richness hotspots₉₀, NFP reserves, pre-NFP reserves, and non-reserved lands represented 206, 27, and 42% of their expected areas, respectively. In the regional salamander hotspots₇₅, NFP reserves, pre-NFP reserves, and non-reserved lands represented 120, 118, and 70% of their

expected areas, respectively. Thus, salamander hotspots (with both definitions) had much more reserved land than expected and much less non-reserved.

Concordance of mollusc and salamander richness patterns

Local richness of salamanders and molluscs was significantly, though extremely weakly, correlated ($F = 7.135$, $P = 0.008$, $r^2 = 0.029$). The hotspots₉₀ of mollusc regional richness encompassed 37% of the salamander regional richness hotspots₉₀. The salamander regional richness hotspots₉₀, however, encompassed only 16% of the mollusc regional richness hotspots₉₀. The overlap of hotspots₇₅ between taxa was greater with the hotspots₇₅ of mollusc regional richness encompassing 94% of the hotspots₉₀ of salamander regional richness and 61% of the hotspots₇₅ of salamander regional richness. The hotspots₇₅ of salamander regional richness encompassed 69% of the mollusc regional richness hotspots₉₀ and 45% of the mollusc regional richness hotspots₇₅.

Species representation

The 100 simulations of reserve locations resulted in 17–35 mollusc species and two to nine salamander species being represented within the reserves. The actual NFP reserves contained 32 mollusc species and eight salamander species; with only one

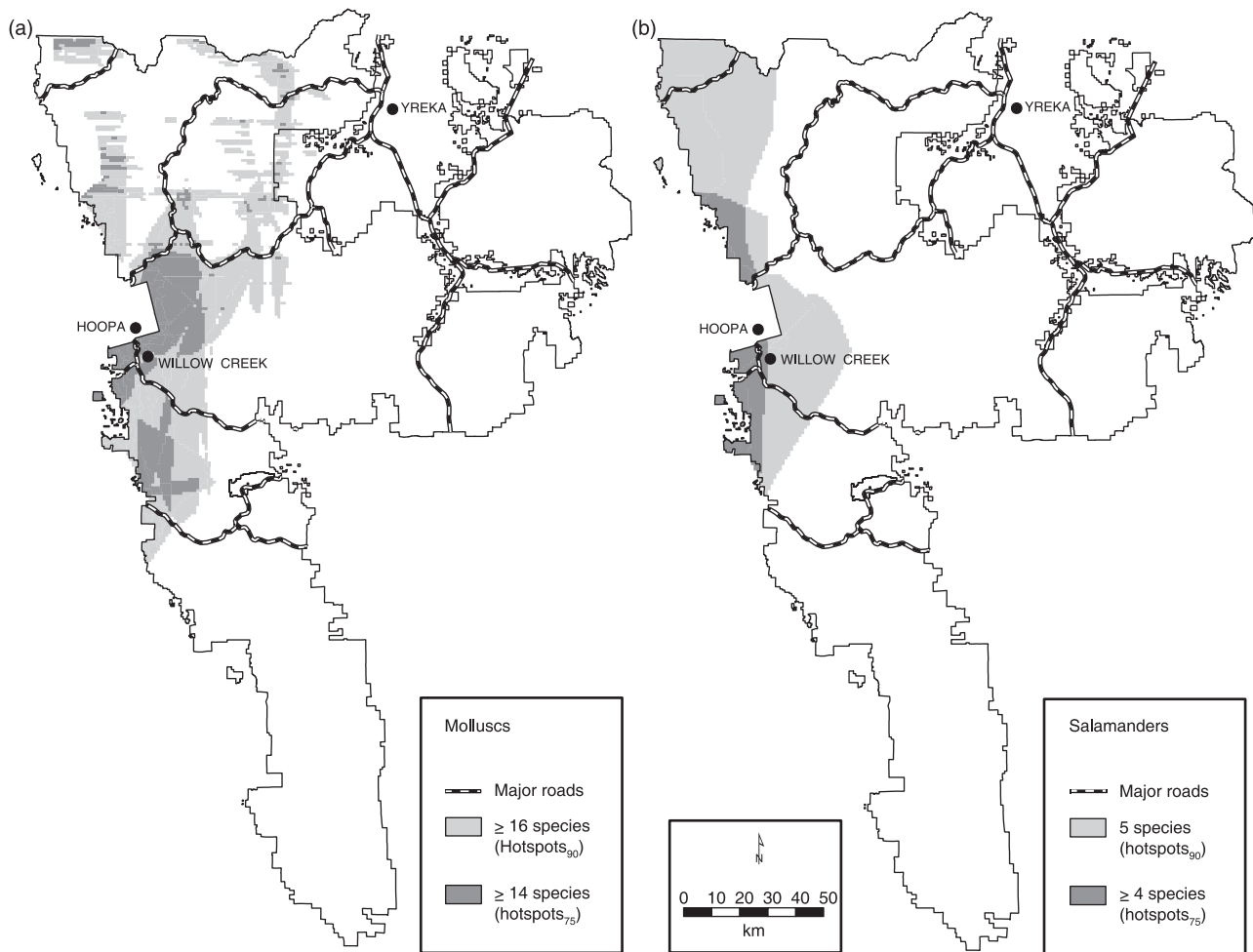


Figure 3 (a) Mollusc regional richness hotspot₉₀ and hotspot₇₅ and (b) salamander regional richness hotspot₉₀ and hotspot₇₅. All areas mapped at 1-km² resolution. For purposes of presentation a few linear areas (1 km high and = 3 km long) identified as hotspots were removed from part a.

and seven simulated reserves ranking higher than the actual reserve system's representation of mollusc species and salamander species, respectively. Although both taxa had species represented much greater than would be expected by chance, only 68% and 73% of all mollusc and salamander species were detected in reserves, respectively. However, when including pre-NFP reserves, reserved lands contained 39 mollusc species (83% of all mollusc species) and 10 salamander species (91% of all salamander species).

Distribution of rare species

Of the 47 mollusc species detected, 26 were encountered at only one or two plots and were considered 'rare'. Three rare mollusc species occurred within the hotspots₉₀ of mollusc regional richness while 1.7 would be expected based on the areal extent of this hotspot. Within the hotspots₇₅ of regional mollusc richness, 14 rare mollusc species were detected, while 7.5 rare species would be expected. Of the 11 species of salamanders detected, four were considered rare. None of the rare salamanders were found in the hotspots₉₀ and two were found in the hotspots₇₅. Thus, rare molluscs were more common in hotspots than were salamanders.

DISCUSSION

Patterns

The Klamath-Siskiyou region is considered extremely ecologically diverse (DellaSala *et al.*, 1999; Ricketts *et al.*, 1999), primarily because of its geological and climatic history. For example, regarding the Klamath-Siskiyou region's flora, Coleman & Kruckeberg (1999) stated 'following the increased aridity of the Miocene, the KS [Klamath-Siskiyou] region, with its benign climate, became the refuge for elements of a shrinking warm-temperate flora in the Far West. Second, the spatial isolation, coupled with a long-persisting high level of habitat diversity, created a multiplicity of settings for both the genesis of new species and the persistence of relictual species.' For terrestrial molluscs and salamanders, the most species-rich areas were discovered in the western/northwestern portion of our study area (Figs 2 and 3), an area that overlaps the area Stebbins & Major (1965; see their Fig. 2) identified as having a high frequency of relictual plant species. The KS region is not uniformly biologically rich. Instead, it contains both hotspots and 'coldspots' of molluscs and

salamanders. The hotspots of mollusc and salamander diversity may be locations where climate, geology, and biotic conditions have remained most stable within our study area.

Concordance of hotspots among taxa

For two disparate taxa we found a statistically significant, but biologically weak, correlation ($r^2 = 0.029$) in their *local* richness, a low (16–37%) overlap in the hotspots₉₀ of their *regional* richness and a low (45%) to moderate (61%) overlap in their hotspots₇₅ of *regional* richness. Several studies have compared taxa hotspots (e.g. Rey Benayas & Montaña, 2003; Sætersdal *et al.*, 2003), but a number of such comparisons have also failed to establish concordance (e.g. Tardif & Des Granges, 1998; Allen *et al.*, 2001; Ricketts *et al.*, 2002). Our finding that the regional mollusc hotspots₇₅ encompassed 61% of the regional salamander hotspots₇₅, but only 45% overlap vice versa provides equivocal support to our contention that both taxa may have responded similarly to historical, and perhaps contemporary, factors. Moritz *et al.* (2001) found that snails and insects were good surrogates for vertebrates in Australia, but not vice versa. Molluscs in our study were better surrogates for salamander hotspots₇₅ than vice versa. Based on our findings, and those of Moritz *et al.* (2001), it would be of interest to evaluate the degree to which molluscs might serve as surrogates for other vertebrates in our study area as well.

Protection

The authors of the NFP did not evaluate patterns of, or set conservation targets for, terrestrial mollusc or salamander richness, or species representation, when deciding on their conservation strategy and subsequent designation of reserves. Our analyses, however, showed that the reserves they delineated, together with pre-existing reserves, disproportionately protected hotspots₇₅ of local and regional richness for both taxa. Hotspots₇₅ of both taxa at the local and regional scale, and hotspots₉₀ of both taxa at the regional scale were represented by reserves more than non-reserved lands. Although *regional* richness hotspots₉₀ of both taxa were disproportionately associated with reserved lands, those locations where *local* richness was greatest (local hotspots₉₀) were not disproportionately associated with reserved lands. Therefore, our sample suggests that the current reserve network does not provide disproportionate protection to those local areas richest in species of terrestrial molluscs and salamanders. Because such areas are rare (e.g. 4.5% and 9.4% of sampled plots for molluscs and salamanders, respectively) and some are currently protected, additional measures to ensure their protection should not be prohibitively burdensome. However, other similarly rich locales may exist and a comprehensive plan to protect them will require either additional sampling or predicting their locations using a model.

Both mollusc and salamander species representation was much greater in NFP reserves than would be expected by chance. Thus, although NFP reserves were not designed using species representation data, our evaluation suggests that reserves designed

largely using quantitative data from the northern spotted owl included a disproportionately large percentage of the mollusc and salamander species that occur in the region. The existing reserve network included 83% of all mollusc species and 91% of all salamander species detected during our surveys. In relation to systematic conservation planning, Margules & Pressey (2000) stated that 'the extent to which targets for representation and persistence have already been achieved in existing reserves has to be determined.' Although the NFP described no species representation or persistence targets for most species, we have provided an estimate of the degree to which existing reserves represent terrestrial mollusc and salamander species. Estimating persistence of species within these taxa will be a much more difficult task — as many of the species have never been the subject of even basic natural history studies.

Rare molluscs were disproportionately (nearly twice the number expected) found in regional hotspots₉₀ and hotspots₇₅. Even so, 12 of the 26 rare mollusc species were not found within the mollusc regional hotspots. Similarly, only two of the four rare salamanders were found in regional salamander hotspots₇₅, and none in the regional salamander hotspots₉₀. Thus, a large proportion of the rare species within each taxon would go unprotected with conservation plans developed only around such hotspots (see Lennon *et al.*, 2004). Eleven rare molluscs were found in plots on unreserved lands, although only four of those species were found exclusively in unreserved lands. None of the rare salamanders were found in plots on unreserved lands.

To our knowledge, this is the first quantitative, empirical, evaluation of the NFP's effectiveness at sheltering species diversity. The degree to which species inside NFP reserves are protected, however, will vary depending on the type and extent of management activities that occur within these reserves, and to varying extents, outside of reserves. For example, low-intensity prescribed fire treatments might provide long-term protection against catastrophic, stand-replacing wildfires. In contrast, post-wildfire timber salvage operations might remove or destroy forest legacy components that may provide refugia for these taxa (see Franklin *et al.*, 1997; Franklin *et al.*, 2000).

We, and others working within the NFP area, have had a unique opportunity to evaluate the relative contributions of reserves established for different purposes. Although species conservation is often an added benefit of pre-NFP reserve designation, the inspirational, scenic, and recreational values they provide humanity are more often the reasons for such designations. NFP reserves, in contrast, were specifically designed for species conservation. The NFP attempted to adequately protect native species while simultaneously providing commodities from federal lands. Although the authors of the NFP evaluated > 1000 species when considering the number and location of reserves, their final selection of reserves (NFP reserves) closely match the reserve network recommended by Thomas *et al.* (1990) and USDI (1992) for the northern spotted owl. If the NFP reserves represent a large-scale plan largely for the northern spotted owl, as well as other organisms having smaller spatial requirements than the owl, our findings suggest that owl conservation provides some umbrella protection for areas with high species richness of

terrestrial molluscs and salamanders in national forests in northern California. In terms of species representation, NFP reserves (and thus the northern spotted owl as a focal species for conservation) do fairly well; but taken together with pre-NFP reserves represent a large percentage (> 80%) of terrestrial mollusc and salamander species.

Conclusions

The locations of hotspots of mollusc and salamander richness are likely a function of ancient and contemporary factors. The Northwest Forest Plan's reserve network provides more protection for both local and regional richness hotspots₇₅ than would be expected by chance. Similarly, the NFP reserve network encompasses much higher species representation of terrestrial molluscs and salamanders than would be expected by chance. Therefore, the northern spotted owl serves as a reasonable coarse-filter umbrella species for the taxa we evaluated. Our findings and those of Caro (2003) suggest that conservation plans designed around umbrella species can be effective. Nonetheless, the current reserve network should not be considered the optimal reserve network for the taxa we studied. We found that current reserves do not disproportionately protect the local richness hotspots₉₀ of either terrestrial molluscs or salamanders, and that some of the rarest species do not receive protection under the existing reserve network. Due to the limited dispersal ability of these taxa, areas containing the highest local species richness are of conservation importance. An evaluation of the biotic and abiotic factors associated with both local and regional hotspots could provide land managers a template of desired future conditions to maintain or encourage.

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